A framework for quantifying the magnitude and variability of community responses to global change drivers

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Keywords: beta diversity | community dissimilarity | convergence | divergence | multivariate analysis | non-metric multidimensional scaling | rank abundance curve | species composition

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A framework for quantifying the magnitude and variability of community responses to global change drivers

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Key words: beta diversity; community dissimilarity; convergence; divergence; multivariate analysis; non-metric multidimensional scaling; rank abundance curve; species composition.

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INTRODUCTION

Ecologists are currently tasked with predicting how communities will respond to a wide variety of global changes including chronic resource alterations (Smith et al. 2009) and shifting biodiversity (Chapin et al. 2000). As such, the field of experimental global change ecology is rapidly expanding, with many experiments aiming to understand how different *global change*

Box 1 Glossary of terms

global change driver (GCD): A human-driven exogenous perturbation that changes abiotic (e.g., resources, temperature, pollution) or biotic (e.g., invasive species) conditions typically occurring as widespread chronic presses. Global change drivers can also change the magnitude or frequency of episodic natural disturbance regimes (fire suppression, hurricanes).
community composition: The identity and abundance of all species in a given space and time.
among treatments: Comparing the community composition of treatment and control plots. This concept is similar to turnover beta diversity (see Vellend 2001, Anderson et al. 2011), however, instead of comparing how species composition of plots changes along a gradient, it is mean dissimilarity of the treatment plots from the control plots.
within treatments: Comparing the community composition of plots within a treatment. This is variation beta diversity (see Vellend 2001, Anderson et al. 2011).
convergence: Communities become more similar to one another in composition through time.
divergence: Communities become less similar to one another in composition through time.
parallel change: Communities that change compositionally through time, but do not converge or diverge.
rank abundance curves (RAC): A display of species abundance distributions that presents each species' abundance on the vertical axis and its rank in abundance (ordered from highest to lowest abundance) on the horizontal axis.

drivers (GCDs) will impact communities (see Box 1 for definitions of italicized words). However, many of these studies focus on univariate responses only, such as summary measures of community diversity (e.g., richness). As noted by Collins et al. (2008), these univariate approaches can obfuscate complex community changes. Instead, a multivariate approach that considers *community composition* in its entirety can be more informative, if it can be done in a generalizable manner. Indeed, changes in community composition can be systematically studied using distance-based dissimilarity metrics, recently popularized as useful for measures of beta diversity (Anderson et al. 2006, 2011).

Dissimilarity metrics enable the study of both the magnitude and the predictability of community responses by comparing experimental replicates both *among treatments* as well as *within treatments*. Community dissimilarity of replicates among treatments is informative for understanding the magnitude of community change corresponding with a change in environmental conditions, while community dissimilarity of replicates within treatments can indicate the predictability of community change. For example, Inouye and Tilman (1988, 1995) found that replicate tallgrass prairie plant communities receiving high-level nitrogen additions diverged from one another, while those receiving less nitrogen converged. Likewise, Houseman and colleagues (2008) found patterns of *convergence* among replicate grassland plant communities with disturbance and *divergence* with fertilization treatment. Finally, Koerner and colleagues (*unpublished manuscript*) found increasing levels of community divergence among replicates with higher levels of nitrogen and phosphorus additions. Thus, one might infer from these three studies that depending on the degree of fertilization, communities may become more heterogeneous making it more difficult to predict community responses. Studying broad patterns enables generalizations and comparison across studies, as well as enhancing our ability to identify the mechanisms that lead to patterns of convergence or divergence, as characterized in previous succession and community assembly studies (Clements 1936, Leps and Rejmanek 1991, Fukami 2010, Weiher et al. 2011).

Understanding patterns of community change over time (Clements 1916, Gleason 1926) and identifying mechanisms of change (Connell and

Slatyer 1977) was an early and consistent focus of ecological research. Prach and Walker (2011) suggest re-visiting the successional literature to increase our understanding of how GCDs alter communities. GCDs are environmental perturbations that typically result in chronic resource alterations, but do not clear space (Smith et al. 2009) to initiate primary or secondary successional dynamics. However, the processes, mechanisms, and terminology of GCD induced community change are the same as those used to describe succession. As with succession, the list of potential mechanisms for global change driven community alterations is extensive (Connell and Slatyer 1977, Walker and Chapin 1987, Pickett and McDonnell 1989). While ultimately it is desirable to know the mechanisms by which a community changed, mechanisms can be case specific and prevent generalizations. Across the plethora of global change experiments, it might be more informative to first determine whether there are clear patterns of community change in response to GCDs. After patterns of community responses have been identified, specific mechanisms may more easily be elucidated.

Here, we present a new framework for studying GCD caused community changes by simultaneously using multivariate community dissimilarity metrics and rank abundance curves (Fig. 1). We propose that comparing dissimilarity of replicates both among and within treatments will give insight into both the magnitude and the predictability or repeatability of community change. One drawback of such an approach is that it is difficult to understand what aspect of the community was altered using dissimilarity metrics alone. To overcome this potential limitation, we demonstrate how integrating *rank abundance curves* (RACs) with community dissimilarity metrics can be used to identify concomitant changes in community structure (Fig. 1). Towards this end, we hypothesize how species changes reflected in RACs might change community dissimilarity metrics both among and within treatments, and present examples of community studies that use multivariate methods to highlight this new framework. Lastly, we suggest future directions for this framework and provide testable hypotheses for the field.

Detecting the Magnitude and Predictability of Community Change Using Dissimilarly Metrics

There are two important measures of dissimilarity among replicates (Houseman et al. 2008; Figs. 1 and 2): (1) the mean dissimilarity of replicates *among treatments* (i.e., do control and treated replicates have similar communities?) and (2) the mean dissimilarity of replicates *within treatments* (i.e., do control or treated replicates have different community variability?). The first measure, mean dissimilarity of replicates among treatments, is the separation between treatment centroids in multivariate community space and is similar to the concept of turnover beta diversity (see Box 1; Vellend 2001, Anderson et al. 2011). The second, mean dissimilarity of replicates within treatments, is the dispersion of replicates around the treatment centroid in multivariate community space (Clarke 1993) and is the same as variation beta diversity (see Box 1; Vellend 2001, Anderson et al. 2011). Both measures of variability are affected by the species present and their abundances (Clarke 1993).

Using multivariate measures to determine changes in the composition of communities is a way to quantify beta diversity (Legendre et al. 2005, Anderson 2006, Bacaro et al. 2012, Legendre and De Cáceres 2013). More traditionally, beta diversity has been calculated directly from alpha and gamma diversity (Whittaker 1960, Tuomisto 2010*a*). Beta diversity is highly influenced by local alpha diversity and regional gamma diversity (Anderson et al. 2011, Chase et al. 2011, Kraft et al. 2011). However, because our framework is for an experimental examination of GCDs on communities, we are less concerned with how changes in alpha or gamma diversity will affect beta diversity. We consider gamma diversity to be the total species pool for the experiment and thus static, and we consider alpha diversity to be the number of species in a treatment and therefore changeable over time. While studies typically find that GCDs reduce alpha diversity (Chalcraft et al. 2008, Powell et al. 2013), these reductions are often not drastic. For example, across 40 grassland sites, three years of NPK additions resulted on average a loss of two species (Borer et al. 2014), and such minor losses are commonly found (see Zavaleta et al. 2003,

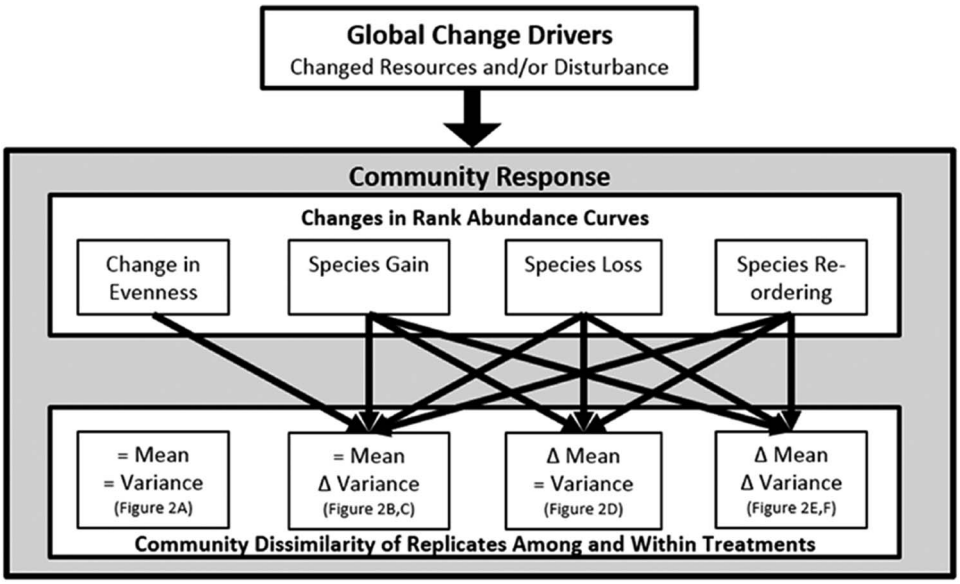

Fig. 1. Conceptual diagram illustrating a new approach to studying community responses. Global change drivers alter abiotic or biotic conditions that influence a wide range of potential mechanisms that change communities. Using rank abundance curves in conjunction with community dissimilarity measures provides insight into the magnitude and predictability of community change. Within the community response gray box, black arrows indicate our hypotheses about how changes in rank abundance curves result in changes in community dissimilarity patterns (see Table 1 for details). "= Mean" indicates low dissimilarity between treatment and control replicates and high overlap in multivariate community space. "Δ Mean" indicates high dissimilarity of replicates among treatments and decreased overlap in multivariate community space. "= Variance" indicates similar dissimilarity of replicates within treatments and similar dispersion of replicates around the centroid in multivariate community space. Lastly, "Δ Variance" indicates changes in the dissimilarity of replicates within treatments and a different degree of dispersion in multivariate community space.

Avolio et al. 2014). However, if within an experiment there are very large changes in alpha diversity, null models may be a useful tool to understand the true changes in beta diversity that are not influenced by gamma or alpha diversity (Chase et al. 2011, Chase and Myers 2011, Kraft et al. 2011). In this paper, because we are interested in both aspects of beta diversity simultaneously (turnover and variation), we are moving away from the tortured beta diversity language and simply discuss multivariate patterns below.

We envision eight ways that individual replicates can differ from one another in their dissimilarity both among and within treatments and demonstrate these patterns in a hypothetical multivariate community space (Bray and Curtis 1957) for easy visualization (Fig. 2). While investigating community changes using dissimilarity metrics and visualizing differences is a method commonly used in community ecology (see Houseman et al. 2008), here we suggest that looking at changes in dissimilarity of replicates among and within treatments simultaneity can be particularly informative for GCD experiments. As shown in Fig. 2A, control and treated replicates can have the same mean and variance, representing the null hypothesis that a GCD had no affect community composition. Treated replicates can also have the same mean, but with greater variance among replicates (divergence) with no evidence for multiple new community states (Fig. 2B1) or where some replicates are more similar to each other than other sets of replicates, possibly indicating multiple new community states (Fig. 2B2). A third scenario occurs when there are equal means and a reduction in variance among

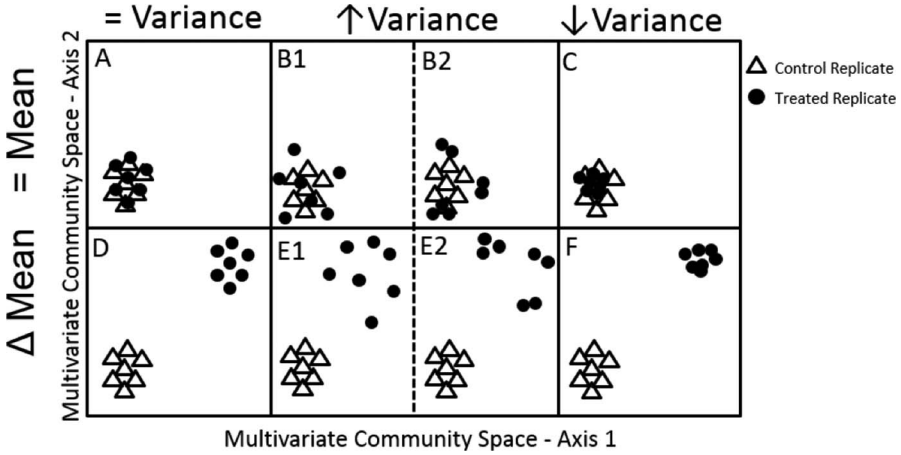

Fig. 2. Plots for the eight possible ways community dissimilarity of replicates among and within treatments could change in response to global change drivers (mean in rows, variance in columns). Here we utilize a hypothetical experiment with two treatments, control (white triangles) and treated (black circles), shown in multivariate space. (A) No change in mean or variance of replicates both among and within treatments. (B) No change in mean but increased variance (divergence), with no pattern (B1) or with several distinct new community types (B2). (C) No change in mean but reduced variance (convergence). (D) Change in mean with no change in variance (parallel change). (E) Change in mean and increased variance (divergence), with no distinct pattern (E1) or several new community states (E2). (F) Change in mean and reduced variance (convergence).

replicates (convergence; Fig.2C). These four variance responses could also be accompanied by a change in mean (Fig. 2D–F). Regardless of the pattern in variability among treated replicates, both stochastic and deterministic processes can cause either community convergence or divergence (Chase and Myers 2011). Thus, it is important to note that the observed pattern among replicates does not necessarily indicate the nature of the mechanism that brought about the community change, but it does provide important quantification of the pattern that may be generalizable across studies.

By investigating the variability of the community response among replicates (Fraterrigo and Rusak 2008, Murphy and Romanuk 2012), patterns can be identified that give insight into the repeatability and predictability of community change. An observed pattern of *parallel change* or convergence among replicates would suggest that all treated replicates respond the same way and community changes may be predictable. Conversely, if all replicates diverged from one another in their community composition, then the community response may be difficult or impossible to predict.

Measuring and Analyzing Patterns of Community Dissimilarity

There have been many influential papers on multivariate community analyses. Here we briefly review the steps necessary for such analyses, from creating a dissimilarity matrix to performing statistical tests. The first step is to carefully select an appropriate dissimilarity metric and create a dissimilarity matrix of all replicates to one another (Anderson et al. 2006, Anderson et al. 2011). We suggest using abundance data and an associated dissimilarity metric (e.g., Bray-Curtis dissimilarity) over presence/absence data for three reasons. First, abundance data also allows for the subsequent examination of rank abundance curves (see below for details). Second, abundance data is more sensitive to detecting deterministic changes in community composition compared with presence/absence data (Segre et al. 2014). Third, calculating dissimilarity from presence/absence data is highly dependent differences in on alpha diversity (Chase et al. 2011). Next, it is helpful to visualize differences in community composition of replicates via nonmetric multidimensional scaling (NMDS) or

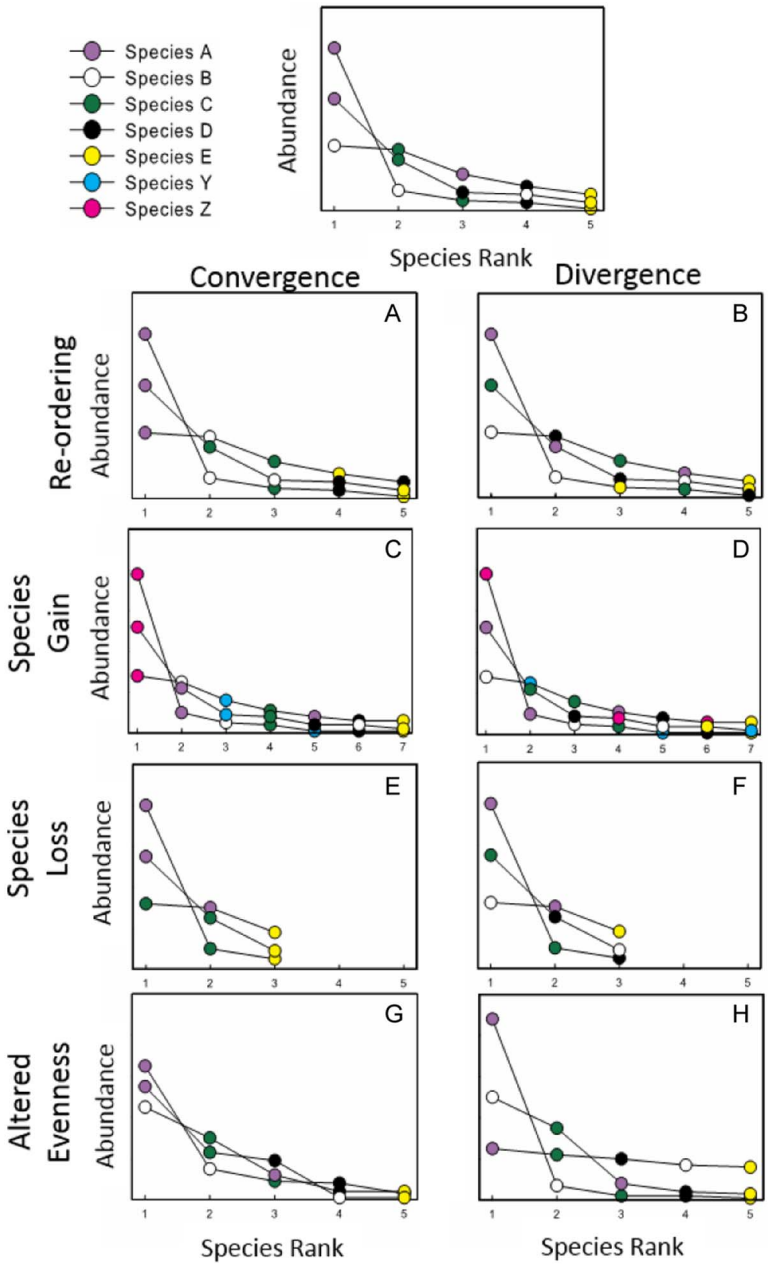

Fig. 3. There are four ways the rank abundance curves (RAC) could change in response to the community changes identified in Fig. 2. Panels A–H should be compared with the control plot on top of the Fig. First, species reordering occurs when all the same species remain in the community but their order changes (A, B). Both a gain (C, D) and a loss of species (E, F) from the community occurs when species immigrate into or go extinct from the community. Note that both of these changes necessitate species re-ordering unless they happen in the tail of the RAC. Lastly, there can be a change in evenness only (G, H). Note that the scale of the *x*-axis changes. Depending on the nature and degree of the change to the RAC, these four basic changes a community can lead to changes in community dissimilarity both among and within treatments (see Table 1).

principal coordinates analysis (PCO or PCoA; Legendre and Legendre 2012). Both analyses will produce a plot showing symbols representing replicates appearing close together if their local communities are similar (based on the dissimilarity metric chosen) or far apart if their communities are dissimilar (see Fig. 4 for examples). After the patterns have been discerned, it is desirable to test whether differences among treatments in both their mean (among treatment differences) and dispersion of replicates (within treatment differences) are statistically significant. To test for differences of replicates among treatments (difference of centroids), permutational multivariate analysis of variance (PERMANOVA) is perhaps the most popular method. Anderson and Walsh (2013) recently demonstrated that with balanced experimental designs, PERMANOVA is relatively insensitive to changes in variance among groups. There are a multitude of different approaches to test for differences in dispersion of replicates within treatments (Tuomisto 2010*b*, Anderson et al. 2011); however, many do not allow statistical tests because they produce only one estimate of variation (Anderson 2006). Two approaches that do allow statistical testing are permutational tests for homogeneity of variance (Anderson 2001, 2006) or general linear model-based approaches (Wang et al. 2012). Because of their widespread use and known capabilities for detecting patterns of convergence and divergence, overall we advocate use of PERMANOVA to test for changes in mean among treatments and permutational tests for homogeneity of variance to test for changes in dispersion.

Integrating Rank Abundance Curves with Community Dissimilarity Metrics

We argue that measuring community dissimilarity among replicates in response to GCDs offers insight into the magnitude and predictability of community change. However, it is possible to lose valuable information when using community dissimilarity metrics alone (Collins et al. 2008), because it is unclear how the community changed. One way to understand these community-level changes is to examine changes in specific species that drive the community response (e.g., Houseman et al. 2008), but this approach has limited application across systems. A second more generalizable approach is to pair community dissimilarity analyses with examination of changes in the community's species abundance distribution, which describe the relative abundances of all constituent species within a community. Species abundance distributions are useful as visualization tools to help ecologists understand how communities are structured and are relatively easy to create using commonly collected species abundance data (McGill et al. 2007, Ulrich et al. 2010). Rank abundance curves (RACs; e.g., Fig. 3), are a type of species abundance distribution first introduced in the mid-20th century (MacArthur 1957, Whittaker 1965). Here, we suggest using RACs to isolate specific aspects of community change in response to GCDs (McGill et al. 2007, Collins et al. 2008; Fig. 1). Once the patterns of change in the RAC have been identified and classified (see below; Fig. 1), mechanisms responsible for that change can be more easily explored. Further, by identifying changes in RAC, the findings from studies are more generalizable, facilitating comparisons across systems, GCDs, and experiments.

There are four ways that GCDs can modify RACs (Fig. 3) within a replicate following a perturbation: (1) RACs can be altered due to species re-ordering; that is, the rank of species can change because one or more species have either decreased or increased in abundance. Additionally, RACs can be modified by the (2) loss and/or (3) gain of species. While re-ordering alone can occur without a gain or loss of species, it is important to recognize that the loss or gain of any species that is not the lowest rank must co-occur with species reordering. Lastly, RACs can be changed by (4) shifts in species evenness; that is, the shape of the curve can become steeper (greater dominance) or flatter (greater evenness). We hypothesize that for each of the eight possible patterns of community change (Fig. 2), there are a limited number of ways the RAC can change, and present a table of testable hypotheses integrating changes in community dissimilarity and RACs (Table 1), by comparing a control with a GCD treatment. For example, we hypothesize that the re-ordering, gain or loss of only rare species in the treated replicates will change the variability among replicates within treatments but not the mean (Table 1), while for common

Table 1. Hypothesized relationships between rank abundance curves and the multivariate community similarity of control and treated replicates (means and variances). For each multivariate community pattern (change in mean and variance) we hypothesize whether a change in one aspect of the rank abundance curve *alone* could give rise to that pattern, and our unit of consideration is each replicate. Please note that these changes are not mutually exclusive. Community abundance data, not presence/absence data, are necessary for these types of analyses.

	Rank abundance curve responses			
Multivariate communitypattern	Altered evenness	Sp. gains	Sp. losses	Sp. re-ordering
= mean, = variance (Fig. 2A)	No	No	No	No
= mean, ↑ variance (Fig. 2B)	Yes	Yes†	Yes†	Yes†
= mean, ↓ variance (Fig. 2C)	Yes	Yes†	Yes†	Yes†
Δ mean, = variance (Fig. 2D)	No	Yes‡	Yes‡	Yes‡
Δ mean, ↑ variance (Fig. 2E)	No	Yes¶	Yes¶	Yes§
Δ mean, ↓ variance (Fig. 2F)	No	Yes¶	Yes	Yes

† Will occur only if the response is limited to rare species.
‡ Will occur only if the same species respond similarly in all replicates.
§ Will only occur if different rare species become dominant across replicates.
¶ This type of change necessitates species re-ordering.

species, all three processes could result in shifts in mean and changes in dispersion (Table 1). Many of these scenarios are not mutually exclusive and all four modifications to the RAC can occur simultaneously.

Overall, there is great interest in determining the mechanisms underlying community responses to GCDs. However, without a clear understanding of how communities shift in response to GCDs (e.g., loss of dominance, turnover of functional types), these mechanisms will likely be difficult to determine. Key to understanding patterns of community responses to global change is correctly measuring the species pool. Indeed, recent studies have shown that patterns of diversity responses to GCDs can be altered by the area sampled alone (Chase and Knight 2013, Powell et al. 2013). As suggested by Chase and Knight (2013) collecting abundance data is potentially key to obtaining unbiased effect sizes of GCDs on communities, and may make researchers less prone to draw conclusions from probabilistic sampling effects. Further, RACs necessitate collecting abundance data. Additionally, with a thorough understanding of the patterns of change in RACs in response to GCDs, future experiments can be designed to test potential mechanisms underlying any observed response, either deterministic or stochastic.

Case Studies

We present six examples of the changes in multivariate community space illustrating the application of our conceptual framework. For each case study, we describe observed changes in community dissimilarity mean and variance among replicates between control and treatments and graph the non-metric multi-dimensional scaling plots for each case study comparing the control plots to those altered by a treatment (Fig. 4). Where possible, we also detail how changes in the RACs led to the observed changes. Lastly, we explore how understanding these changes in RACs can lead to hypothesized mechanisms determining community responses. Where possible we use examples where the treatment is a GCD, however as GCD studies examining multivariate community shifts are relatively rare, this was not possible for all scenarios.

No change in mean, no change in variance (Fig. 4A)

We hypothesized that no change in mean or variance would occur when there is no change in the RAC (Table 1). Johnson and Fleeger (2009) examined the responses of salt marsh benthic annelids to nutrient additions and large predator removals in two pairs of tidal creeks in Plum Island Estuary, Massachusetts, USA. They found no consistent changes in the abundance of any species and also observed no change in the community composition among treatments, as measured by shifts in NMDS plots and analyzed using ANOSIM.

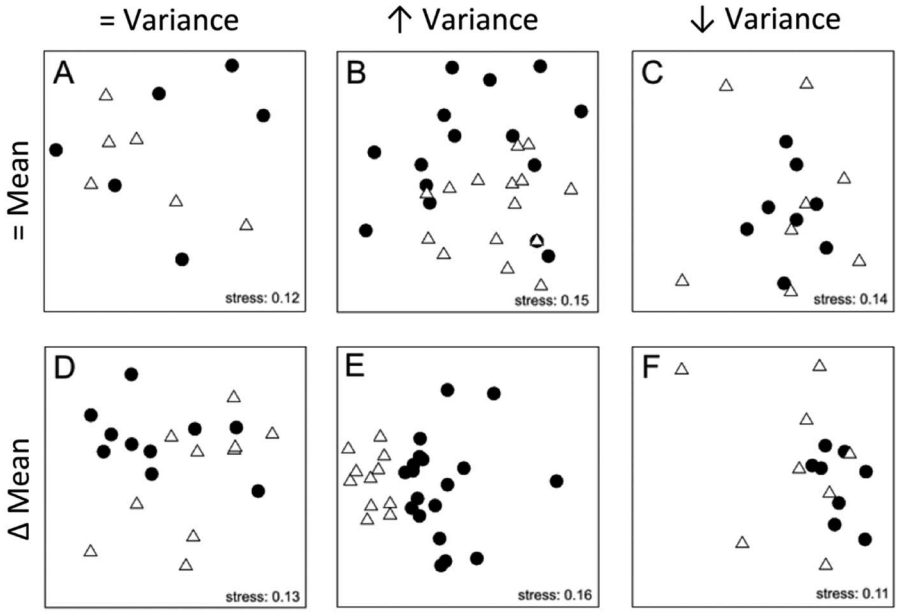

Fig. 4. Non-metric multi-dimensional scaling plots for each of the case studies comparing the control plots (white triangles) to those altered by a treatment (black circles). (A) Community responses to large predator removals in tidal creeks (triangles = ambient fish; circles = fish removals); (B) marine benthic mollusk community responses to the presence of a gas platform (triangles = far from platform; circles = near platform); (C) grassland plant community responses to a one-time, high intensity disturbance (triangles = undisturbed; circles = disturbed); (D) Silver Fir forest tree community responses to recovery from 10 years of heavy exploitation in the mid-1900s (triangles = light management; circles = complete abandonment); (E) native ant community responses to Argentine ant invasions (triangles = never invaded; circles = invaded); (F) grassland arthropod community responses to addition of invasive grass litter (triangles = no litter added; circles = litter added).

No change in mean, increase in variance (Fig. 4B)

We hypothesized that no change in mean with an increase in variance should be observed with species reordering, loss, or gain, but only when these changes occur for rare species, or with changes in species evenness (Table 1). Terlizzi et al. (2009) examined changes in the composition of marine benthic mollusk communities that were either located adjacent to or far from gas drilling platforms in the Ionian Sea off of the coast of Italy. They observed no change in mean (as measured by PERMANOVA), but an increase in variance (as measured by PERMDISP, a permutational test for homogeneity of variance) of mollusk communities located adjacent to the gas platforms. This increase in variance was likely caused by greater environmental heterogeneity due to fouling from the drilling platforms onto the sea floor. The increased environmental heterogeneity caused species gains or losses from individual sampling locations (Bevilacqua, *personal communication*).

No change in mean, decrease in variance (Fig. 4C)

We hypothesized that no change in mean with a decrease in variance should be observed with species reordering, loss, or gain, but only when these changes occur for rare species, or with changes in species evenness (Table 1). Houseman et al. (2008) examined changes in species composition in response to a one-time removal of biomass following solarization and herbicide application in grasslands in southwest Michigan, USA. In response to the one-time disturbance, there was no change in the centroid in multivariate community space (as measured by PERMANOVA) with a decrease in the variance (as measured by PERMDISP). This pattern appeared to have been driven by a decrease in species evenness in the disturbed plots.

Change in mean, no change in variance (Fig. 4D)

We hypothesized that a change in mean with no change in variance should be observed with species reordering, loss, or gain, but only when these processes occur to the same extent in all replicates (Table 1). Sitzia et al. (2012) examined changes in the richness and composition of tree species in two Silver Fir forests in Italy that were either abandoned or lightly managed after a common history of heavy exploitation. Sitzia et al. (2012) observed changes in species number and a similar reordering of species with abandonment as compared to plots that were lightly managed, which corresponded with a change in the centroid in multivariate community space (as measured by PERMANOVA) but no change in the variance (as measured by PERMDISP).

Change in mean, increase in variance (Fig. 4E)

We hypothesized that community divergence accompanied by a change in the mean in multivariate community space can be observed with species reordering when a different species becomes dominant in each plot or by differential species gain or loss, which must necessarily be accompanied by species reordering (Table 1). Cooling et al. (2012) examined the effects of the invasive Argentine ant on native ant communities across New Zealand. In ant communities that never had Argentine ants, the native ant community showed little variability between sites (Cooling et al. 2012). However, when Argentine ants invaded an area, the native ant community drastically altered the mean in multivariate community space and increased the variability, as measured by PERMDISP. Cooling et al. (2012) found a decrease in ant species richness with Argentine ant invasions, indicating species loss. The species that were lost due to Argentine ant invasion varied among the plots, resulting in differential species loss and specific species reordering for each plot.

Change in mean, decrease in variance (Fig. 4F)

We hypothesized that community convergence accompanied by a change in the mean in multivariate community space can be observed with species reordering when the same species becomes dominant in each plot or by similar species gains or losses, which must necessarily be accompanied by species reordering (Table 1). Wolkovich (2010) examined changes in the composition of scrubland arthropod communities in response to invasive grass litter additions in southern California, USA, which resulted in a shift in the centroid in multivariate community space (as measured by PERMANOVA) and a decrease in the variance (as measured by PERMDISP). With this last example, we show how changes in RACs link to changes in community dissimilarity (Fig. 5). The shifts in multivariate space were driven by the systematic loss of less common morphospecies, gain of new morphospecies, and increased abundances of the same morphospecies (i.e., reordering) across all treatment replicates (Fig. 5).

Conclusions and Future Directions

We are in a new age of experimental ecology, where a multitude of studies are being conducted around the world to understand how GCDs are altering communities and ecosystem function. The number of meta-analyses synthesizing the effects of precipitation manipulations (Wu et al. 2010), nutrient additions (Suding et al. 2005, Elser et al. 2007), temperature changes (Rustad et al. 2001, Wu et al. 2010), invasion (Liao et al. 2008), and carbon dioxide increases (Curtis and Wang 1998) on communities are indicative of the plethora of experiments. Many studies focus on measures of ecosystem function, and we suggest that community composition of replicates should also always be recorded, as it is relatively inexpensive and can be very informative. We contend that future community analyses in GCD experiments should assess multivariate patterns of replicates among and within treatments. Our framework presents a generalizable approach to studying the magnitude, predictability and trajectory of community change in response to global change by integrating measures of community dissimilarity with rank abundance curves. Additionally, enhancing our understanding of the predictability of community responses to GCDs might lead to a more predictive framework for ecosystem responses to GCDs, because ecosystem responses are typically driven by changes in community structure (Smith et al. 2009, Isbell et al. 2013, Avolio et al. 2014). Because many global change studies collect both community and ecosystem data, we can begin to

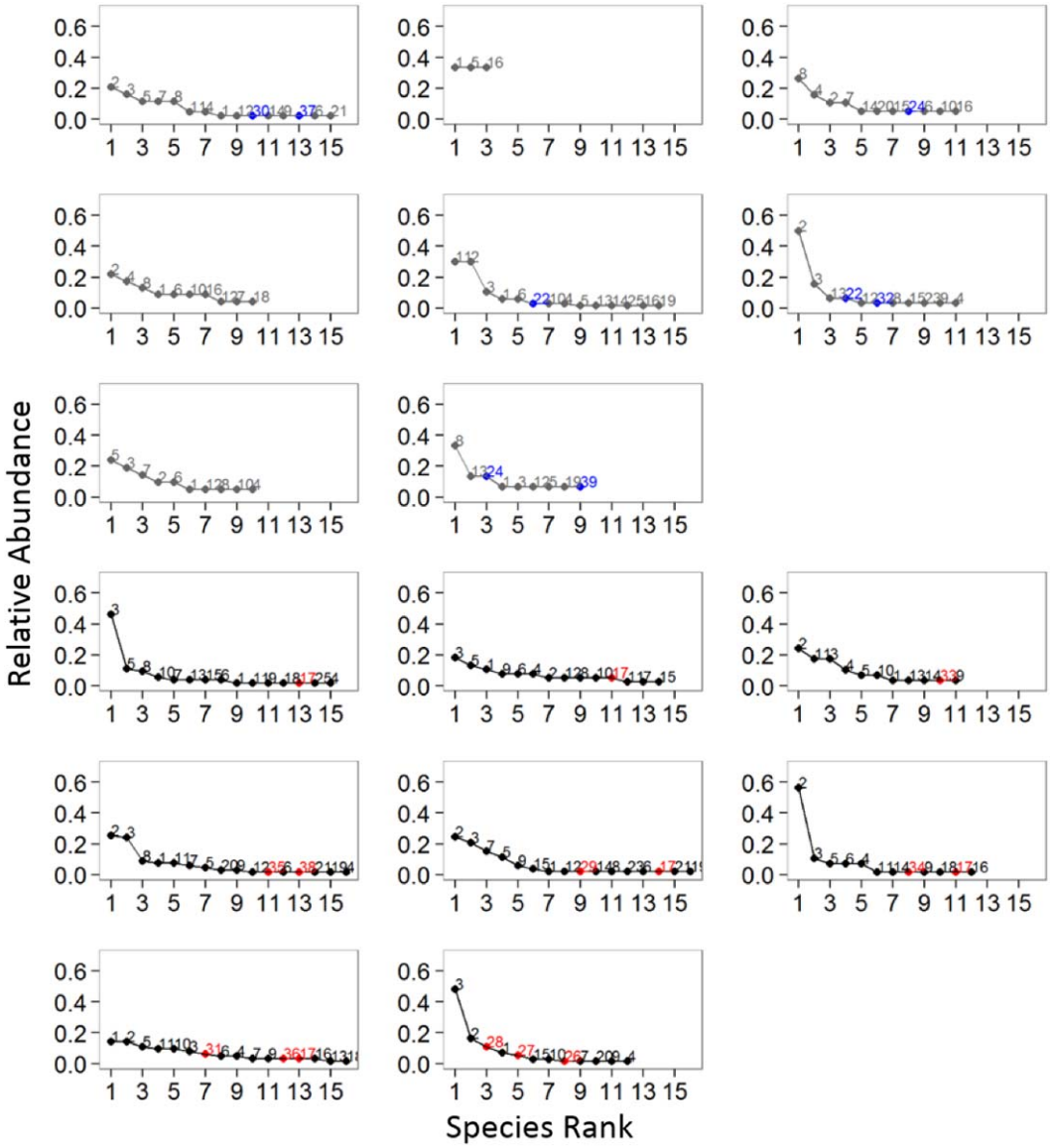

Fig. 5. RAC changes for the eight control and treated replicates in the Wolkovich (2010) paper. Each graph is a replicate. The top eight gray line-graphs are the control replicates, and the bottom eight black line-graphs are the treated replicates. Each morphospecies was numbered (39 total species) and its relative abundance was plotted according to its rank in each replicate. A blue number is a morphospecies that was only present in the control replicates, and red number is morphospecies that was only found in the treated replicates.

synthesize across GCD studies and link patterns of community convergence or divergence with alterations in ecosystem functioning using our framework.

Many global change studies only manipulate a single GCD, and seldom compare observed community changes to different GCDs (e.g., comparing N addition to drought). However, such comparisons are informative (Winfree et al. 2009, Murphy and Romanuk 2012, Tilman et al. 2012, Murphy and Romanuk 2014) and experiments are increasingly studying multiple global change drivers in single experiments (Shaw et al. 2002). Future studies should focus on what

conditions result in divergence, convergence or parallel change of communities. For instance, does alteration of only one GCD commonly result in patterns of convergence while simultaneous alteration of two or more GCDs commonly results in patterns of divergence? Do particular GCDs (e.g., nitrogen or drought) lead to convergence, divergence or parallel change? Are ecosystems that have greater gamma diversity more prone to change compared with species poor communities? Our framework will facilitate more comparisons and greater synthesis across studies and drivers, because we are less focused on the mechanisms, which can be specific to study systems, organism type, and GCD manipulated. Instead we are interested in patterns of community change, and the generality of these patterns. Ultimately, our new framework will advance the field of community ecology global change studies in two ways: (1) by helping ecologist identify the trajectory, magnitude and predictability of community change and (2) providing a framework to synthesize community responses across ecosystems and GCDs.

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Literature Cited

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46.

Anderson, M. J. 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62:245–253.

Anderson, M. J., et al. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. Ecology Letters 14:19–28.

Anderson, M. J., K. E. Ellingsen, and B. H. McArdle. 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters 9:683–693.

Anderson, M. J., and D. C. Walsh. 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? Ecological Monographs 83:557–574.

Avolio, M. A., S. E. Koerner, K. J. La Pierre, K. R. Wilcox, G. W. T. Wilson, M. D. Smith, and S. L. Collins. 2014. Changes in plant community composition, not diversity, during a decade of nitrogen and phosphorus additions drive aboveground productivity in a tallgrass prairie. Journal of Ecology 102:1649–1660.

Bacaro, G., M. Gioria, and C. Ricotta. 2012. Testing for differences in beta diversity from plot-to-plot dissimilarities. Ecological Research 27:285–292.

Borer, E. T., et al. 2014. Herbivores and nutrients control grassland plant diversity via light limitation. Nature 508:517–520.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecology Monographs 27:325–349.

Chalcraft, D. R., S. B. Cox, C. Clark, E. E. Cleland, K. N. Suding, E. Weiher, and D. Pennington. 2008. Scale-dependent responses of plant biodiversity to nitrogen enrichment. Ecology 89:2165–2171.

Chapin, F. S., et al. 2000. Consequences of changing biodiversity. Nature 405:234–242.

Chase, J. M., and T. M. Knight. 2013. Scale-dependent effect sizes of ecological drivers on biodiversity: why standardised sampling is not enough. Ecology Letters 16:17–26.

Chase, J. M., N. J. B. Kraft, K. G. Smith, M. Vellend, and B. D. Inouye. 2011. Using null models to disentangle variation in community dissimilarity from variation in α-diversity. Ecosphere 2:art24.

Chase, J. M., and J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. Philosophical Transactions of the Royal Society B 366:2351–2363.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117–143.

Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. Carnegie Institution of Washington, Washington, D.C., USA.

Clements, F. E. 1936. Nature and structure of the climax. Journal of Ecology 24:252–284.

Collins, S. L., K. N. Suding, E. E. Cleland, M. Batty, S. C. Pennings, K. L. Gross, J. B. Grace, L. Gough, J. E. Fargione, and C. M. Clark. 2008. Rank clocks and plant community dynamics. Ecology 89:3534–3541.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111:1119–1144.

Cooling, M., S. Hartley, D. A. Sim, and P. J. Lester. 2012. The widespread collapse of an invasive species: Argentine ants (*Linepithema humile*) in New Zealand. Biology Letters 8:430–433.

Curtis, P. S., and X. Wang. 1998. A meta-analysis of

elevated CO_2 effects on woody plant mass, form, and physiology. Oecologia 113:299–313.

Elser, J. J., M. E. S. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecology Letters 10:1135–1142.

Fraterrigo, J. M., and J. A. Rusak. 2008. Disturbance-driven changes in the variability of ecological patterns and processes. Ecology Letters 11:756–770.

Fukami, T. 2010. Community assembly dynamics in space. Pages 45–54 *in* H. A. Verhoef and P. J. Morin, editors. Community ecology: processes, models, and applications. University Press Oxford, Oxford, UK.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53:7–26.

Houseman, G. R., G. G. Mittelbach, H. L. Reynolds, and K. L. Gross. 2008. Perturbations alter community convergence, divergence, and formation of multiple community states. Ecology 89:2172–2180.

Inouye, R. S., and D. Tilman. 1988. Convergence and divergence of old-field plant communities along experimental nitrogen gradients. Ecology 69:995–1004.

Inouye, R. S., and D. Tilman. 1995. Convergence and divergence of old-field vegetation after 11 years of nitrogen addition. Ecology 76:1872–1887.

Isbell, F., P. B. Reich, D. Tilman, S. Hobbie, S. Polasky, and S. Binder. 2013. Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. Proceedings of the National Academy of Sciences USA 110:11911–11916.

Johnson, D. S., and J. W. Fleeger. 2009. Weak response of saltmarsh infauna to ecosystem-wide nutrient enrichment and fish predator reduction: a four-year study. Journal of Experimental Marine Biology and Ecology 373:35–44.

Kraft, N. J., et al. 2011. Disentangling the drivers of β diversity along latitudinal and elevational gradients. Science 333:1755–1758.

Legendre, P., D. Borcard, and P. Peres-Neto. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. Ecological Monographs 75:435–450.

Legendre, P., and M. De Cáceres. 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecology Letters 16:951–963.

Legendre, P., and L. Legendre. 2012. Numerical ecology. Third edition. Elsevier, Amsterdam, The Netherlands.

Leps, J., and M. Rejmanek. 1991. Convergence or divergence: What should we expect from vegetation succession? Oikos 62:261–264.

Liao, C., R. Peng, Y. Luo, X. Zhou, X. Wu, C. Fang, J. Chen, and B. Li. 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. Global Change Biology 177:706–714.

MacArthur, R. H. 1957. On the relative abundance of bird species. Proceedings of the National Academy of Sciences USA 43:293–295.

McGill, B. J., R. S. Etienne, J. S. Gray, D. Alonso, M. J. Anderson, H. K. Benecha, M. Dornelas, B. J. Enquist, J. L. Green, and F. He. 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. Ecology Letters 10:995–1015.

Murphy, G. E. P., and T. N. Romanuk. 2012. A meta-analysis of community response predictability to anthropogenic disturbances. American Naturalist 180:316–327.

Murphy, G. E., and T. N. Romanuk. 2014. A meta-analysis of declines in local species richness from human disturbances. Ecology and Evolution 4:91–103.

Pickett, S. T., and M. McDonnell. 1989. Changing perspectives in community dynamics: a theory of successional forces. Trends in Ecology and Evolution 4:241–245.

Powell, K. I., J. M. Chase, and T. M. Knight. 2013. Invasive plants have scale-dependent effects on diversity by altering species-area relationships. Science 339:316–318.

Prach, K., and L. R. Walker. 2011. Four opportunities for studies of ecological succession. Trends in Ecology and Evolution 26:119–123.

Rustad, L. E., J. L. Campbell, G. M. Marion, R. J. Norby, M. J. Mitchell, A. E. Hartley, J. H. C. Cornelissen, and J. Gurevitch, and GCTE-NEWS. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543–562.

Segre, H., R. Ron, N. De Malach, Z. Henkin, M. Mandel, and R. Kadmon. 2014. Competitive exclusion, beta diversity, and deterministic vs. stochastic drivers of community assembly. Ecology Letters 17:1400–1408.

Shaw, M. R., E. S. Zavaleta, N. R. Chiariello, E. E. Cleland, H. A. Mooney, and C. B. Field. 2002. Grassland responses to global environmental changes suppressed by elevated CO_2. Science 298:1987–1990.

Sitzia, T., G. Trentanovi, M. Dainese, G. Gobbo, E. Lingua, and M. Sommacal. 2012. Stand structure and plant species diversity in managed and abandoned silver fir mature woodlands. Forest Ecology and Management 270:232–238.

Smith, M. D., A. K. Knapp, and S. L. Collins. 2009. A framework for assessing ecosystem dynamics in

response to chronic resource alterations induced by global change. Ecology 90:3279–3289.

Suding, K., S. L. Collins, L. Gough, C. M. Clark, E. E. Cleland, K. L. Gross, D. G. Milchunas, and S. Pennings. 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proceedings of the National Academy of Sciences USA 102:4387–4392.

Terlizzi, A., M. J. Anderson, S. Bevilacqua, S. Fraschetti, M. Włodarska-Kowalczuk, and K. E. Ellingsen. 2009. Beta diversity and taxonomic sufficiency: Do higher-level taxa reflect heterogeneity in species composition? Diversity and Distributions 15:450–458.

Tilman, D., P. B. Reich, and F. Isbell. 2012. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. Proceedings of the National Academy of Sciences USA 109:10394–10397.

Tuomisto, H. 2010*a*. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. Ecography 33:2–22.

Tuomisto, H. 2010*b*. A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. Ecography 33:23–45.

Ulrich, W., M. Ollik, and K. I. Ugland. 2010. A meta-analysis of species–abundance distributions. Oikos 119:1149–1155.

Vellend, M. 2001. Do commonly used indices of β-diversity measure species turnover? Journal of Vegetation Science 12:545–522.

Walker, L. R., and F. S. Chapin. 1987. Interactions among processes controlling successional change. Oikos 50:131–135.

Wang, Y., U. Naumann, S. T. Wright, and D. I. Warton. 2012. mvabund: an R package for model-based analysis of multivariate abundance data. Methods in Ecology and Evolution 3:471–474.

Weiher, E., D. Freund, T. Bunton, A. Stefanski, T. Lee, and S. Bentivenga. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. Philosophical Transactions of the Royal Society B 366:2403–2413.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:279–338.

Whittaker, R. H. 1965. Dominance and diversity in land plant communities: numerical relations of species express the importance of competition in community function and evolution. Science 147:250–260.

Winfree, R., R. Aguilar, D. P. Vázquez, G. LeBuhn, and M. A. Aizen. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. Ecology 90:2068–2076.

Wolkovich, E. M. 2010. Nonnative grass litter enhances grazing arthropod assemblages by increasing native shrub growth. Ecology 91:756–766.

Wu, Z., P. Dijkstra, G. W. Koch, J. Peñuelas, and B. A. Hungate. 2010. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Global Change Biology 17:927–942.

Zavaleta, E. S., R. Shaw, N. R. Chiriello, B. D. Thomas, E. E. Cleland, C. B. Field, and H. A. Mooney. 2003. Grassland responses to three years of elevated temperature, CO_2, and N deposition. Ecological Monographs 73:585–604.